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REVIEW

# Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea*

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ABSTRACT: Detailed reproductive data are now available for 210 of the ca 600 identified scleractinian reef coral species. The majority (131 species) are hermaphroditic broadcast spawners, although hermaphroditic brooders (11 species), gonochoristic broadcasters (37 species), and gonochoristic brooders (7 species) have also been reported. Characteristics of sexuality and mode of reproduction are generally conservative within species, genera, and even families, although some exceptions occur. Variation in timing or mode of reproduction in allopatric populations may represent adaptations to local environmental conditions or indicate problems in the taxonomy of some groups. Synchronous spawning of numerous species occurs on the Great Barrier Reef, while asynchrony among and within species has been observed in the Red Sea, Caribbean, Central Pacific, Hawaii, and southern Japan. Sexual reproduction is the primary means for successful recruitment for some coral populations, while asexual processes may be the dominant or sole means of recruitment for these same species at the limits of their ranges. Recruitment success of different reproductive strategies may vary within and between localities, and is mediated by both biotic (predation, competition) and abiotic (environmental variability, disturbance) factors. Data on reproductive patterns and recruitment success may be applied to coral reef management practices.

## INTRODUCTION

Until the last decade, the majority of data on coral reproduction were anecdotal and incomplete observations based on short-term and sporadic studies (see review by Fadlallah 1983). This situation is not surprising, in light of the remoteness of tropical coral reefs from most universities and research facilities, and the logistical difficulties of studying corals in situ. However, a number of recent investigations have been published based on continuous monitoring of field populations, as well as histological and laboratory examination of individuals. Previous generalizations and perceived trends may now be re-examined, as data for a greater number of species over a wide geographic range have become available.

Detailed reproductive data have been reported for ca 40 % of the known species from the tropical Pacific (studies from the Great Barrier Reef, Guam, Palau, Enewetak, Hawaii, Okinawa, and Panama), 30 % of Caribbean coral species, and 6 % of Red Sea species. These studies provide information on coral sex (hermaphroditism vs gonochorism), mode of reproduction (brooding vs broadcast spawning), and timing of reproduction (seasonality, periodicity, and synchrony). Certain patterns of reproduction and recruitment are now discernible from these data. In this paper, we review data for 210 scleractinian species, and compare reproductive processes observed in the Caribbean, eastern Pacific, Hawaii, Central Pacific, southern Japan, Great Barrier Reef, and Red Sea. As data for more taxa and

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regions become available, additional (or different) patterns and trends may emerge.

The study of coral reproduction has advanced through numerous theses and dissertations over the last 10 yr, as well as from concerted group efforts, most notably on the Great Barrier Reef of Australia. The major pattern that has developed from the Great Barrier Reef studies is one of remarkable similarity and synchrony of reproductive activity among coral species. The majority (90 %) of species studied there broadcast spawn gametes annually, during the week following the full moon in the austral spring (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). Data from other regions (the Caribbean, Red Sea, Central Pacific, Hawaii, and southern Japan) show different patterns, with considerable variation in mode, timing, and synchrony among species. In addition, populations of the same species reported from 2 or more regions may display different reproductive traits. Globally, corals display great plasticity in their life history characteristics. These data are summarized for each region in Table 1, and across regions in Tables 2, 3 and 4.

## REPRODUCTION IN GENERAL

Corals reproduce both sexually and asexually. Sexual reproduction involves the process of gametogenesis, which may require from a few weeks for sperm, to over 10 mo for eggs. Spawning and subsequent fertilization of eggs by sperm results in small, presumably genetically unique, dispersive propagules (planula larvae) which may settle, metamorphose and develop into primary polyps. Asexual reproduction is also common in many scleractinian species, and may occur through fragmentation (see review by Highsmith 1982), polyp bail-out (Goreau & Goreau 1959, Sammarco 1982), or asexual production of planulae (Stoddart 1983). Asexual processes result in clonal propagules (genetic replicates of adult colonies) which, if derived from fragments, have the apparent advantages of large size and locally adapted genotypes.

### Sexual reproduction in corals

#### Hermaphroditism vs gonochorism

In hermaphroditic species, ovaries and spermaries may develop on the same mesentery (most favids and mussids), on different mesenteries within the same polyp (most pocilloporids and acroporids; see Fig. 1), in different polyps within the same colony (e. g. *Cladopsammia rolandi*; de Lacaze-Duthiers 1897 in Fadlallah 1983), or at different times within the same colony (e. g. *Stylophora pistillata*; Loya 1976, Rinkevich & Loya 1979a).

Corals can be simultaneous or sequential hermaphrodites (see discussion in Fadlallah 1983). Two species, *Stylophora pistillata* and *Goniastrea favulus*, exhibit protandrous development (Rinkevich & Loya 1979b, Kojis & Quinn 1981a). The only report (Duerden 1902) of true protogyny, in which the colony functions first as a female and becomes hermaphroditic in subsequent years, has been questioned (Szmant 1986). Most hermaphroditic corals exhibit annual protogyny, where eggs develop prior to spermary formation during a reproductive season.

Mixed breeding systems have been described for a brooding species, *Porites astreoides*, in which 26 % of colonies examined were hermaphroditic, 28 % had only female gonads, and 46 % were sterile (Chornesky & Peters 1987). In *Galaxea fascicularis*, some colonies are female and some are hermaphroditic, but eggs in the latter apparently serve only to provide buoyancy for the sperm packets (Heyward et al. 1987, Harrison 1989).

Hermaphroditism is advantageous when the probability of finding (or, in the case of sedentary corals, proximity to) members of the opposite sex is low, and self-fertilization is possible. Heyward & Babcock (1986) found varying levels of success in self-crosses in 4 coral species (0 % in *Montipora digitata*, 1.5 to 16 % in *Acropora tenuis* and *Goniastrea aspera*, and 26 to 89 % in *Goniastrea favulus*). In experiments performed during spawning events on Guam during the summers of 1987 and 1988, no viable planulae developed from mixing gametes from the same individuals in *Acropora irregularis* or *A. humilis*, while nearly 100 % of the embryos resulting from self-fertilized eggs of *Acropora tenuis* developed successfully (Richmond 1989, unpubl.). Barriers to self-fertilization apparently break down with time after spawning for some species, but not for others (Heyward & Babcock 1986, Richmond unpubl.)

Numbers of gonochoristic and hermaphroditic species within each region are summarized in Table 2. Within regions, hermaphrodites range from 60 to 100 % of reported species. Globally, the majority (68 %) of coral species studied are hermaphroditic (Table 3).

#### Brooding vs spawning

Fertilization may take place within the maternal polyp (brooding), or externally in the water column after gametes are shed (broadcast spawning). Species which broadcast spawn outnumber brooders in the Pacific regions and the Red Sea (Table 2). However, brooding may be the predominant mode of reproduction in the Caribbean. Overall, for the present data

Table 1. Reproductive characteristics of corals from the Caribbean Sea, Great Barrier Reef, Central Pacific, Hawaii, Okinawa, eastern Pacific, and Red Sea. Symbols – Sex: H, hermaphroditic; G, gonochoric; x, unknown. Mode: S, spawner; B, brooder; * possibly sterile. Timing: month and lunar day of gamete release (spawners) or planulation (brooders) [month is divided into phases: 1, new moon, 3, first quarter, 5, full moon, 7, last quarter; 2, 4, 6 and 8 indicate intermediate lunar phases (after Shlesinger & Loya 1985)]; w, winter; sp, spring; sr, summer; f, fall; yr, year-round; x, unknown

| Species | Sex | Mode | Timing | Source |
|---|---|---|---|---|
| **Caribbean** | | | | |
| ACROPORIDAE | | | | |
| *Acropora cervicornis* | H | S | Jul/Aug, 6–7 | Szmant-Froelich (1984), Szmant (1986) |
| *Acropora palmata* | H | S | Aug | Szmant-Froelich (1984), Szmant (1986) |
| AGARICIDAE | | | | |
| *Agaricia agaricites* | H | B | sp | Duerden (1902), Van Moorsel (1983) |
| *Agaricia crassa* | x | B | sp | Vaughan (1910) |
| *Agaricia fragilis* | x | B | sr | Mavor (1915) |
| *Agaricia humilis* | H | B | yr | Van Moorsel (1983) |
| FAVIIDAE | | | | |
| *Diploria strigosa* | H | S | Aug, 7 | Szmant-Froelich (1984) |
| *Favia fragum* | H | B | yr | Duerden (1902), Vaughan (1910) |
| | | | yr, 3–5 | Szmant-Froelich (1984), Szmant (1986) |
| | | | | Szmant-Froelich et al. (1985) |
| *Manicina areolata* | H | B | sp | Wilson (1888) in Fadlallah (1983) |
| | | | yr | Duerden (1902) |
| *Montastrea annularis* | H | S | Aug, 7/Sep, 7 | Szmant-Froelich (1984), Szmant (1986) |
| *Montastrea cavernosa* | G | S | Aug | Szmant-Froelich (1984), Szmant (1986) |
| MEANDRINIDAE | | | | |
| *Meandrina* (= *Meandra*) *areolata* | x | B | Jul/Aug, 3–8 | Boschma (1929), Yonge (1935) in Fadlallah (1983) |
| MUSSIDAE | | | | |
| *Isophyllia* sp. | G? | B | sp | Duerden (1902) |
| *Mycetophyllia ferox* | H | B | Feb–Mar | Szmant-Froelich (1984), Szmant (1986) |
| PORITIDAE | | | | |
| *Porites astreoides* | H | B | May–Jun | Vaughan (1910), Szmant-Froelich (1984) |
| | | | Jan–Sep | Szmant (1986) |
| | (or female only) | | yr, 6–8 | Chornesky & Peters (1987) |
| *Porites porites* | G? | B | Nov–Feb | Tomascik & Sander (1987) |
| | (some hermaphroditic) | | | |
| SIDERASTREIDAE | | | | |
| *Siderastrea radians* | H | B | yr | Duerden (1902) |
| | G | B | yr? | Szmant-Froelich (1984), Szmant (1986) |
| *Siderastrea siderea* | G | S | Jul–Sep | Szmant-Froelich (1984), Szmant (1986) |
| TROCHOSMILIIDAE | | | | |
| *Dendrogyra cylindrus* | G | S | Aug | Szmant-Froelich (1984), Szmant (1986) |
| | 6G:10H:3x | 12B:7S | | |
| **Pacific** | | | | |
| Great Barrier Reef | | | | |
| ACROPORIDAE | | | | |
| *Acropora aculeus* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Acropora aspera* | H | S | seasonal | Bothwell (1981) |
| *Acropora austera* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Acropora cerealis* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Acropora cuneata* | H | B | sp–sr | Bothwell (1981) |
| *Acropora cytherea* | H | S | Oct/Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Acropora digitifera* | H | S | sp–sr | Bothwell (1981) |
| | | | Oct, 6 | Willis et al. (1985) |
| *Acropora divaricata* | H | S | Oct, 6 | Willis et al. (1985) |
| *Acropora elseyi* | H | S | Nov, 6/Dec, 1 | Babcock et al. (1986) |
| | | | Oct, 1/Nov, 6 | Willis et al. (1985) |
| *Acropora florida* | H | S | Nov, 6 | Willis et al. (1985), Wallace (1985b), |
| | | | | Babcock et al. (1986) |
| *Acropora formosa* | H | S | Nov, 5–6 | Babcock et al. (1986) |
| | | | Oct, 6/Nov, 6 | Willis et al. (1985) |
| *Acropora gemmifera* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Acropora grandis* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |

Table 1 (continued)

| Species | Sex | Mode | Timing | Source |
|---|---|---|---|---|
| **Pacific** | | | | |
| Great Barrier Reef | | | | |
| ACROPORIDAE | | | | |
| *Acropora granulosa* | H | S | Feb/Mar | Wallace (1985b) |
| *Acropora horrida* | H | S | sr? | Wallace (1985b) |
| *Acropora humilis* | H | S | sp–sr | Bothwell (1981) |
| | | | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 5–7 | Babcock et al. (1986) |
| *Acropora hyacinthus* | H | S | sp–sr | Bothwell (1981) |
| | | | Oct/Nov, 6 | Willis et al. (1985), Wallace (1985b) |
| | | | Nov, 5–6 | Babcock et al. (1986) |
| *Acropora latistella* | H | S | Sep, 6/Oct, 6 | Willis et al. (1985) |
| | | | Nov, 1 | Babcock et al. (1986) |
| *Acropora longicyathus* | H | S | Nov, 5 | Willis et al. (1985), Wallace (1985b) |
| | | | | Babcock et al. (1986) |
| *Acropora loripes* | H | S | Nov/Dec | Wallace (1985b) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Acropora lutkeni* | H | S | Nov, 6 | Babcock at al. (1986) |
| *Acropora micropthalma* | H | S | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 5 | Babcock et al. (1986) |
| *Acropora millepora* | H | S | sp–sr | Bothwell (1981) |
| | | | Oct, 6/Nov, 5–6 | Willis et al. (1985) |
| | | | Nov, 5–7 | Babcock et al. (1986) |
| *Acropora nasuta* | H | S | Nov, 6–7 | Willis et al.(1985), Babcock et al. (1986) |
| *Acropora nobilis* | H | S | Oct, 6 | Willis et al. (1985) |
| | | | Oct/Nov | Wallace (1985b) |
| | | | Nov, 5–6 | Babcock et al. (1986) |
| *Acropora palifera* | H | B | x | Bothwell (1981) |
| *Acropora pulchra* | H | S | sp–sr | Bothwell (1981) |
| | | | Oct, 6–7 | Willis et al. (1985) |
| | | | Nov, 5 | Babcock et al. (1986) |
| *Acropora robusta* | H | S | sp–sr | Bothwell (1981) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Acropora samoensis* | H | S | Nov, 6 | Willis et al. (1985) |
| *Acropora sarmentosa* | H | S | Nov, 6 | Willis et al. (1985) |
| | | | Feb/Aug/Nov? | Wallace (1985b) |
| | | | Nov, 7 | Babcock et al. (1986) |
| *Acropora secale* | H | S | Nov, 6–7 | Babcock et al. (1986) |
| *Acropora selago* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Acropora solitariensis* | H | S | Oct, 6 | Willis et al. (1985) |
| *Acropora tenuis* | H | S | Oct, 6–7/Nov, 6 | Willis et al. (1985) |
| | | | Nov, 5–6 | Babcock et al. (1986) |
| *Acropora valenciennesi* | H | S | Nov, 6 | Willis et al. (1985) |
| *Acropora valida* | H | S | Oct, 6–7/Nov, 6 | Willis et al. (1985), Wallace (1985b) |
| | | | Nov, 5–6 | Babcock et al. (1986) |
| *Acropora* cf. *variabilis* | H | S | sp–sr | Bothwell (1981) |
| *Acropora* cf. *vaughani* | H | S | Nov, 6 | Willis et al. (1985) |
| *Acropora yongei* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Astreopora microphthalma* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Montipora aequituberculata* | H | S | Oct, 6 | Willis et al. (1985) |
| *Montipora digitata* | H | S | Oct, 5/Nov, 5 | Willis et al. (1985) |
| | | | Nov, 5 | Babcock et al. (1986), Heyward & Collins (1985) |
| *Montipora foliosa* | H | S | Nov, 5 | Babcock et al. (1986) |
| *Montipora hispida* | H | S | Oct/Nov, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Montipora informis* | H | S | Oct, 5 | Willis et al. (1985) |
| *Montipora monasteriata* | H | S | Nov, 5 | Babcock et al. (1986) |
| *Montipora spumosa* | H | S | Nov, 5 | Babcock et al. (1986) |
| *Montipora tuberculosa* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Montipora turgescens* | H | S | Nov, 6 | Babcock et al. (1986) |
| AGARICIIDAE | | | | |
| *Pachyseris rugosa* | G | S | Nov, 5–6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |

Table 1 (continued)

| Species | Sex | Mode | Timing | Source |
|---|---|---|---|---|
| **Pacific** | | | | |
| Great Barrier Reef | | | | |
| AGARICIIDAE | | | | |
| *Pachyseris speciosa* | G | S | Oct, 6–7/Nov, 5–6 | Willis et al. (1985) |
| | | | Nov, 6–7 | Babcock et al. (1986) |
| *Pavona cactus* | G(?) | S(sperm) | x | Marshall & Stephenson (1933) |
| CARYOPHYLLIDAE | | | | |
| *Catalaphyllia jardineri* | G | S | Oct, 6 | Willis et al. (1985) |
| *Euphyllia ancora* | G | S | Oct, 6 | Willis et al. (1985) |
| *Euphyllia divisa* | G | S | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Physogyra lichtensteini* | G | S | Nov, 6 | Willis et al. (1985) |
| | | | | Babcock et al. (1986) |
| DENDROPHYLLIDAE | | | | |
| *Dendrophyllia* sp. | G | B | Dec, 1 | Babcock et al. (1986) |
| *Heteropsammia cochlea* | G | S | Jan–Jun | Fisk (1981) in Harriott (1983a) |
| *Heteropsammia aequicostatus* | G | S | Apr–Jun | Fisk (1981) in Harriott (1983a) |
| *Tubastrea faulkneri* | G | B | Nov, 6–7 | Babcock et al. (1986) |
| *Turbinaria frondens* | G | S | Oct, 6 | Willis et al. (1985) |
| *Turbinaria reniformis* | G | S | Nov, 7 | Willis et al. (1985) |
| FAVIIDAE | | | | |
| *Australogyra zelli* | H | S | Nov, 6 | Willis et al. (1985), Babock et al. (1986) |
| *Barbattoia amicorum* | H | S | Nov, 5–7 | Babcock et al. (1986) |
| *Caulastrea furcata* | H | S | Nov, 5 | Willis et al. (1985), Babcock et al. (1986) |
| *Cyphastrea chalcidium* | H | S | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Cyphastrea micropthalma* | H | S | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Cyphastrea serailia* | H | S | Oct, 6 | Willis et al. (1985) |
| *Diploastrea heliopora* | G | x | x | Harrison (1985) |
| *Echinopora gemmacea* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Echinopora horrida* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Echinopora lamellosa* | H | S | Oct, 6/Nov, 5 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Favia favus* | H | S | Nov/Dec | Harriott (1983a) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Favia lizardensis* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Favia mathaii* | H | S | Nov, 5–6 | Willis et al. (1985) |
| | | | | Babcock et al. (1986) |
| *Favia pallida* (as *F. doreyensis*) | H | S | Dec | Marshall & Stephenson (1933) |
| *Favia pallida* | | | Oct/Nov, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Favia rotumana* | H | S | Nov, 6 | Willis et al. (1985) |
| *Favia stelligera* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Favia veroni* | H | S | Nov, 5–7 | Babcock et al. (1986) |
| *Favites abdita* | H | S | Nov, 6 | Kojis & Quinn (1982), Babcock et al. (1986) |
| | | | Nov, 5–6 | Willis et al. (1985) |
| *Favites bennettae* | H | S | Nov, 5–7 | Babcock et al. (1986) |
| *Favites chinensis* | H | S | Nov, 6 | Willis et al. (1985) |
| *Favites complanata* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Favites flexuosa* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Favites halicora* | H | S | Nov, 6 | Willis et al. (1985), Babcock et al. (1986) |
| *Favites pentagona* | H | S | Oct, 6 | Willis et al. (1985) |
| | | | Nov, 6 | Babcock et al. (1986) |
| *Favites russelli* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Goniastrea aspera* | H | S | Oct, 5–7 | Babcock (1984) |
| | | | Oct, 6–7/Nov, 6 | Willis et al. (1985) |
| | | | Nov, 5–6 | Babcock et al. (1986) |
| *Goniastrea edwardsi* | H | S | Nov, 6 | Babcock et al. (1986) |
| *Goniastrea favulus* (as *G. australensis*) | H | S | Oct/Nov, 5–6 | Kojis & Quinn (1981a), Kojis & Quinn (1982) |
| *Goniastrea favulus* | | | Oct, 6/Nov, 5–6 | Willis et al. (1985) |
| | | | Nov, 5–6 | Babcock et al. (1986) |